ANTHROPOLOGIE • XLII/1 • pp. 53–58 • 2004

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PALAEODEMOGRAPHY AND DENTAL MICROWEAR OF *HOMO HABILIS* FROM EAST AFRICA

ABSTRACT: We have studied the variability of the buccal microwear pattern in the Homo habilis *population from Olduvai Gorge (Tanzania) and East Rudolf (Kenya), as a dietary indicator in fossil hominin species, and its relationship to the age of the individuals analysed. The estimation of the age of the individuals was done by estimating the rate of dental occlusal wear of individuals of known age. The biodemographic population extinction pattern could be analysed, showing great similarities to that observed in other Paleolithic populations. In the studied sample, the results obtained show that the striation density of the buccal microwear pattern is not significantly correlated with the estimated age at death, despite a tendency towards an increase in the number of striations with age can be observed. Further analyses and greater samples are needed to draw meaningful results.*

KEYWORDS: Paleodemography – Buccal microwear – Hominins – Homo habilis

INTRODUCTION

Studies of the microwear pattern of tooth enamel in human populations suggest that the density of the buccal striations depends on the dietary habits (Lalueza *et al.* 1996, Pérez-Pérez *et al.* 1999), and the age and sex of the individuals (Pérez-Pérez *et al.* 1994). Age at death might be of major importance for microwear research since microstriations seem to accumulate through time, from younger age groups, showing fewer striations, to elder groups where the density of striations seems to stabilize (Pérez-Pérez *et al.* 1994), at least on the buccal surface of teeth. Newly formed striations wear down previously formed ones and equilibrium may be reached between new striations and old ones. Presumably this equilibrium would depend on the abrasive potentiality of ingested foods. Another possibility is that such equilibrium would be attained at a specific striation density level, and that certain populations would attain it faster than others depending on their specific dietary habits. Significantly high densities of striations have been described for Sima de los Huesos (Atapuerca, Spain), which in this case might be caused by *post-mortem* wear (Pérez-Pérez *et al.* 1999). In any case, if tooth microwear patterns are dependent on age, dietary inferences need to be drawn from microwear analyses that take into account the age of the individuals. Estimation of age-at-death is usually done using tooth eruption standards built from modern *Homo sapiens* populations (Moorrees *et al.* 1963). However, fossil specimens are frequently misrepresented. Very few *H. habilis* specimens have been aged using tooth eruption sequences (Tobias 1991). Hominin fossil specimens from Olduvai and East Rudolf, as in many other sites of similar time periods, are most frequently represented by incomplete skeletal remains. The presence of complete skulls or long bones is rare, and the majority of the specimens are represented by isolated teeth. In such cases where the fossil sample is poorly represented and clearly biased, a method of age estimation from teeth is required. Recently, a new method of age-at death estimation for worn-down incisors has been proposed (Bermúdez de Castro 2003). Inferences of age-at-death from tooth wear rates require constant rates of occlusal

TABLE 1. Age-at-deaths of immature individuals from the bibliography, estimated by the cited authors using human developmental tables (*OH*, Olduvai Hominid; *ER*, East Rudolf).

Fossil specimen	Age-at-death in years	Reference
OH 7	12	Tobias 1991
OH 13	15	Tobias 1991
OH 16	16.5	Tobias 1991
OH 21	5	Tobias 1991
OH 39	7.2	Tobias 1991
ER 1813	15	Wolpoff 1999

wear, both within and between individuals. Occlusal wear rates depend on dietary habits and food composition, as well as on enamel thickness and cusp morphology, which may vary among populations and species. In this paper, age-at-death estimation based on occlusal wear rates is used to analyse *Homo habilis* paleodemography. Inferences on mortality rates by age groups are driven and some preliminary results on buccal microwear variability with age are discussed.

MATERIALS AND METHODS

The dental samples studied consist of tooth replicas of the original collections curated at the National Museums of Kenya (Nairobi) and Tanzania (Dar es Salaam). *Homo habilis* specimens from the East African sites of Olduvai Gorge (Tanzania) and East Rudolf (Kenya) were studied in order to characterise age-related patterns of buccal microwear in this species. For this purpose, it is absolutely necessary to make estimations of age-at-death of the individuals studied. *Homo habilis* specimens from Olduvai consist of 30 individuals: 23 with dental remains (OH 4, OH 6, OH 7, OH 13, OH 14, OH 15, OH 16, OH 21, OH 24, OH 27, OH 31, OH 33, OH 37, OH 39, OH 40, OH 41, OH 42, OH 44, OH 45, OH 52, OH 55, OH 56, OH 65) and 7 individuals represented by postcranial remains (OH 8, OH 10, OH 35, OH 43, OH 48, OH 49, OH 50) (Tobias 1991). The sample from East Rudolf consists of 5 individuals with cranial and/or dental remains (ER 1805, ER 1813, ER 1470, ER 1590, ER 1802). After well preserved tooth crowns were selected, the initial tooth sample consisted of 121 teeth belonging to 23 individuals spanning from 1.67 to 2.22 my. Then, the fragmented teeth, whose morphology was impossible to distinguish, and the decidual teeth were rejected (5 teeth of 3 individuals: OH 39, OH 40 and OH 42). Therefore, the final sample included 116 permanent teeth belonging to 20 individuals, which represents 96.6% of the initial sample. The samples were classified into three categories of dental development: 1) unerupted teeth, 2) unworn, erupted teeth, and 3) worn, erupted teeth. The teeth were also classified by type (incisors, canines, premolars and molars) and by maxilla (upper and lower).

Replicas of the whole tooth crowns were obtained with *President MicroSystem* Regular Body (Coltène®) polyvinylsiloxane. The standard procedure is fully described in this same issue (Galbany *et al.* 2004). The replicas were sputter coated with gold and observed with Scanning Electron Microscopy. The enamel of the buccal surface of teeth was photographed at 100x magnification, and a constant surface area of 0.56 mm^2 of enamel was cropped on the medial third of the buccal side of the tooth crown, avoiding both the occlusal and cervical thirds (Pérez-Pérez *et al.* 1999). Areas of damaged enamel and areas with presence of enamel prisms or enamel growth lines (Perikymata or Retzius's striae) were discarded (Martínez *et al.* 2004). In addition, the buccal side of the tooth crown was photographed with a digital camera at 2240×1680 pixels of resolution. Crown heights were measured to estimate the age-at-death of each individual. When taking the picture, the buccal side was placed perpendicular to the camera, measuring the crown height from the cemento-enamel junction to the highest point on the occlusal border rim or the highest cusp tip of the tooth. All measurements were made using the Sigma Scan ProV software by SPSS. Descriptive variables, such as the type of tooth and the individual were obtained from the databases of each museum, revised from the descriptive literature published (Tobias 1991, Leakey R. E. F 1971, 1973b, 1974, 2003, Leakey R. E. F., Wood 1973a, Leakey L. S. B. 1959, 1960, 1961a, 1961b, Leakey L. S. B. *et al.* 1964, Leakey M.D. *et al.* 1971, Blumenschine *et al.* 2003, Wolpoff 1999). For materials not published yet, the characterisation of each tooth was made based on standard morphological traits of teeth (Hillson 1996). In order to further increase the sample of individuals with known age-at-death, *H. habilis* specimens not represented by any dentition were also included in the paleodemographic analysis, whenever age-at-death was known from the literature. Unworn teeth from subadult individuals with known ages (*Table 1*), based on standard tables of human dental development and eruption (Moorrees *et al.* 1963), were used as indicators of unworn crown height. To estimate the age-at-death of adult individuals, a tooth wear rate (amount of crown worn-out relative to the unworn height, in mm per year) was calculated for each tooth separately. Tooth wear rates can provide information about

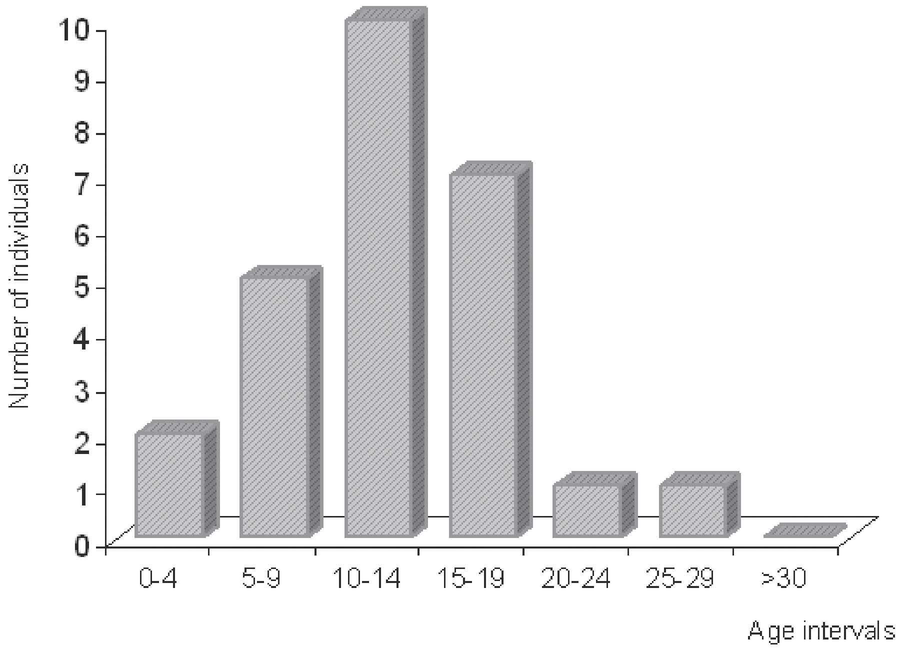

FIGURE 1. Age-at-death distribution of the 26 aged *Homo habilis* individuals.

the approximate age-at-death of individuals within a population (Bermúdez de Castro *et al.* 2003). When a tooth emerges and reaches the occlusal plane of the opposite tooth, it starts to wear. This wear is proportional to the time that the tooth has been in occlusion and depends on the abrasive potential of the diet, the paramasticatory habits, and the enamel width, since dentine wears down faster than enamel. If these factors tend to be stable within a population, they do not produce significant differences in the wear rates among individuals (Pérez-Pérez *et al.* 1994). Some authors have suggested that wear rates depend on tooth class (Wolpoff 1979). In order to confirm this hypothesis, we compared the wear rates among the analysed teeth with a one factor analysis of variance (ANOVA). Independent ages were estimated for each tooth and for pairs of teeth. The wear rates between pairs of teeth (M1-M2, Pm3-Pm4, etc.) were estimated as the ratio between the difference between the worn out crown heights of the two teeth of the pair and the span between their eruption ages. The final age of each individual was calculated as the mean of all the ages obtained with the two procedures (*Table 1*). The estimated age-at-deaths were used in the paleodemographic analysis of the *H. habilis* population studied.

RESULTS AND DISCUSSION

Paleodemographic research is constrained by a series of limitations, which are mainly related to the material studied.

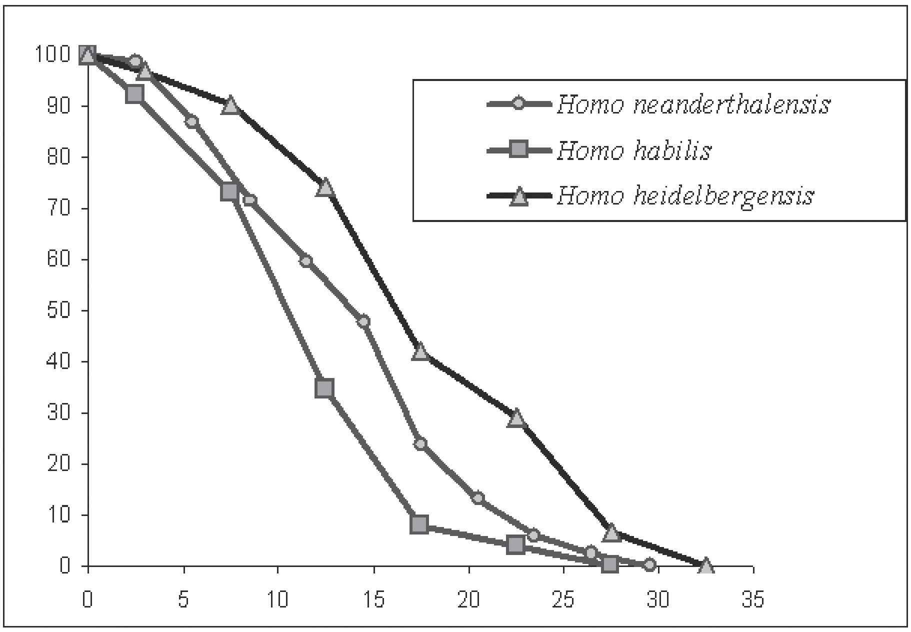

FIGURE 2. Survivorship curves of the *Homo habilis* (Olduvai and East Rudolf), Atapuerca (*Homo heidelbergensis*, Bermúdez de Castro 1997) and Krapina (*Homo neanderthalensis*, Wolpoff 1979) Hominid samples.

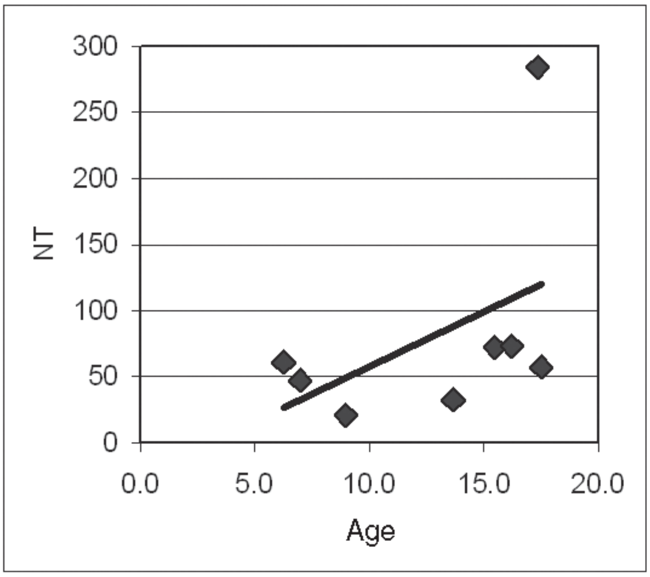

FIGURE 3. Correlation between the density of buccal striations (Y) and the estimated age of the individuals (X) (r=0.465 and P=0.246).

Most frequently the sample studied is not representative of the living population, as is the case in our *Homo habilis* sample, neither represents the population at the time of deposition of the skeletons. In addition, this type of studies are not free from systematic aging error (Weiss 1973, Hassan 1981), which would certainly bias the paleodemographic analyses that are generally based on mortality parameters of the population using the age-at-death estimations. Nevertheless, the estimation of ages made with the studied sample, using the tooth wear rates, has shown to be in accordance with previously known ages. The standard error of this age estimation was calculated for the 6 individuals of known ages, showing a standard error of the difference between actual and estimated age of ±2.8 years. Wear rates by tooth type in the ANOVA tests showed significant differences between the canine and the other teeth. Therefore, a canine wear rate (?? was separately estimated (??2.2161 mm/year) from the other teeth (??0.61444 mm/year). Using these wear rates we could increase the sample of known-age individuals from the 6 subadult ones to 18 individuals with estimated ages (both immature and adults). An additional group of 8 individuals was included in the

TABLE 2. Estimation of the age-at-death of the *Homo habilis* individuals studied using the occlusal wear rates.

	Individual	Estimated age	Sex
1	ER 1590	10.29	
2	ER 1802	8.95	male
3	ER1805	17.67	
4	ER1813	13.42	female
5	OH 4	17.37	male
6	OH 6	13.82	male
7	OH 7	12.44	female
8	OH 8	13.50	
9	OH 13	13.09	female
10	OH 14	14.70	
11	OH 15	25.34	
12	OH 16	12.37	male
13	OH 21	6.994	
14	OH 24	15.00	female
15	OH 27	6.25	
16	OH 33	4.70	
17	OH 37	14.56	male?
18	OH 39	10.31	
19	OH 40	7–9	
20	OH 41	17.5	
21	OH 43	20–24	
22	OH 44	7.2	
23	OH 45	4.7	
24	OH 55	16.40	
25	OH 62	16.24	female
26	OH 65	15.50	female

TABLE 3. Frequency distribution of the age-at-death of the *H. habilis* population studied. Age groups were plotted at 5-year intervals.

0–4 N=2	**5–9 N=5**	**10–14 N=10**	**15–19 N=7**	**20–24 N=1**	**>25 N=1**
OH33	OH21	OH6	OH4	OH43	OH15
OH45	OH27	OH7	OH24		
	OH40	OH 8	OH41		
	OH44	OH13	OH55		
	ER 1802	OH14	OH62		
		OH16	OH65		
		OH37	ER1805		
		OH39			
		ER 1590			
		ER1813			

TABLE 4. Life table of the sample studied. The columns include: 1) Number of deaths in each age interval (D_x); 2) Proportion of the dead in the same intervals (d_x); 3) Survivors of exact age (l_x); 4) Probability of dying in each interval (q_x); 5) Number of years lived by survivors in each interval (L_x), 6) Total years lived after exact age (T_x) and 7) Life expectancy, or average number of years lived after exact age (E_x).

Age intervals	**D_x**	**d_x**	**l_x**	**q_x**	**L_x**	**T_x**	**e^0_x**
0-4	2	7.692	100.000	0.07692308	480.769231	1307.69231	13.0769231
5-9	5	19.231	92.308	0.20833333	413.461538	826.923077	8.95833333
10-14	10	38.462	73.077	0.52631579	269.230769	413.461538	5.65789474
15-19	7	26.923	34.615	0.77777778	105.769231	144.230769	4.16666667
20-24	1	3.846	7.692	0.5	28.8461538	38.4615385	5
25-29	1	3.846	3.846	1	9.61538462	9.61538462	2.5
>30	0	0.000	0.000	0	0	0	0
	26				**1307.69231**		

sample based on the age estimation obtained from the skeletal remains in the literature. Thus, a total sample of 26 *Homo habilis* individuals could be aged. Despite the sample is small for paleodemographic analysis, we have to point up that it is the largest East African sample possible, since all the *Homo habilis* fossil specimens from East Africa available at the moment have been included. The South African specimens are still being analysed and will be shortly added to the sample.

The age distribution of the population (*Figure 1*) indicates a maximum mortality between 10 and 14 years. No individuals are represented in the 0–4 year span, the number of young children is low, and the oldest individual is OH 15 with 25 years. The lack of individuals under four years is probably due to the worse preservation of young individuals and to limitations in the excavation techniques. A significant number of individuals would be expected to die within this span (Weiss 1973), as has been observed in other Plio-Pleistocene populations, such as *Homo heidelbergensis* from Atapuerca (Bermúdez de Castro, Nicolás 1997). The average age-at-death for the specimens of *H. habilis* studied is 12.84 years. While this value is extraordinarily low compared with modern human populations, it is probably higher than expected taking into account the lack of neonate and young specimens (0–4 year). Trinkaus (1995) studied *Homo neanderthalensis* mortality patterns and described that 35% of the population died before they reach 10 years, also assumed that this number would increase to 60% if the preservation bias of the neonates were considered. It seems reasonable to think that neonate mortality during the Pleistocene was at least as high as that of *Homo neanderthalensis*. The lack of older individuals in the studied sample is also unusual, but it has been described as well for *Homo neanderthalensis* from Krapina (Wolpoff 1979). The life table and the survivorship curve of the studied *H. habilis* sample, including both sexes, are shown in *Table 4* and *Figure 2*. Despite the indicated paleodemographic limitations, the mortality patterns observed in *H. habilis* are similar to those described for other ancient populations, although the paleodemographic comparisons between them need to be taken with caution. However, the analyses made suggest that *H. habilis* had higher mortality rates, especially at younger ages, than the more recent fossil species of *Homo*.

TABLE 5. Density of buccal microwear striations in the studied *Homo habilis* sample.

Specimen	**Estimated age**	**Density of microwear striations**
OH 27	6.3	61
OH 21	7.0	47
ER 1802	9.0	21
OH 6	13.7	32
OH 13	15.5	72
OH 62	16.2	73
OH 4	17.4	284
OH 41	17.5	57

When analysing the buccal microwear pattern of *H. habilis*, only 8 (44%) of the 18 individuals that could be studied (120 teeth) had a good tooth enamel preservation in at least one enamel surface on the buccal side of a tooth. Most of the enamel surfaces micrographed were damaged *post-mortem*. The search for well preserved enamel in the *H. habilis* sample still continues, but for the moment only 8 teeth could be included in the analysis. In order to test if the striation pattern was age dependent (Pérez-Pérez *et al.* 1994), we calculated the correlation between the total number of striations observed and estimated age-at-death of the individuals. As indicated, the sample studied is still low, but the correlation obtained is not significant ($r=0.465$, $P=0.246$), despite a slight tendency of the number of striations to increase in older groups (*Figure 3*) is observed. This lack of correlation could be due to a taphonomic effect or to some other *post-mortem* alterations that would affect the enamel preservation. This potential effect was initially controlled for with the exhaustive selection of well preserved enamel surfaces. Other processes might, thus, be also responsible for these alterations, perhaps during life of the individuals (*ante-mortem*), such as an acidic diet (Martínez *et al.* 2001). Further enamel surface analyses are needed to fully characterise the *H. habilis* buccal microwear pattern in future studies.

ACKNOWLEDGEMENTS

This work was funded by the Spanish MCYT project BMC2000-0538. All microscopic images were made at the Serveis Cientifico-tècnics (SCT) of the Universitat de Barcelona.

REFERENCES

BERMÚDEZ DE CASTRO J. M., NICOLÁS M. E., 1997: Palaeodemography of the Atapuerca-SH Middle Pleistocene Hominid Sample. *J. of Hum. Evol.* 33: 333–355.

BERMÚDEZ DE CASTRO J. M., 2003: Rates of anterior tooth wear in Middle Pleistocene Hominins from Sima de los Huesos (Sierra de Atapuerca, Spain) *PNAS* 100, 21: 11992–11996.

BLUMENSCHINE R. J., PETERS C. R., MASAO F. T., CLARKE R. J., DEINO, A. L., RICHARD L. H., SWISHER C. C., STANISTREET I. G., ASHLEY G. M., MC HENRY L. J., SIKES N. E., VAN DER MERWE N. J., TACTIKOS J. C., CUSHING A. E., DEOCAMPO D. M., NJAU J. K., EBERT J. I., 2003: Late Pliocene Homo and hominid land use from Western Olduvai Gorge, Tanzania. *Science* 299: 1217–1221.

GALBANY J., MARTINEZ L. M., PÉREZ-PÉREZ A., 2004: Tooth replication techniques, SEM imaging and microwear analysis in primates: methodological obstacles. *Anthropologie* XLII, 1 (in this issue).

HASSAN F. A., 1981: *Demographic Archaeology*. Academic Press, New York. 95–123 pp.

HILLSON S., 1996: *Dental Anthropology.* Cambridge University Press, London. 373 pp.

LALUEZA C., PÉREZ-PÉREZ A., TURBÓN D., 1996: Dietary inferences through buccal microwear analysis of Middle and Upper Pleistocene human fossils *Amer. J. of Phys. Anthrop.* 100: 367–387.

LEAKEY L. S. B., TOBIAS P. V., NAPIER J. R., 1964: A new species of the genus *Homo* from Olduvai Gorge. *Nature* 202: 7–9.

LEAKEY L. S. B., 1959: A new fossil skull from Olduvai. *Nature* 184: 491–493.

LEAKEY L. S. B., 1960: Recent discoveries at Olduvai Gorge. *Nature* 188: 1050–1052.

LEAKEY L. S. B., 1961a: New finds at Olduvai Gorge. *Nature* 189: 649–650.

LEAKEY L. S. B., 1961b: The juvenile mandible from Olduvai. *Nature* 191:417–418.

LEAKEY L. S. B., LEAKEY M. D., 1964: Recent discoveries of fossil hominids in Tanganyika: at Olduvai and near Lake Natron. *Nature* 202: 5–6.

LEAKEY M. D., CLARKE R. J., LEAKEY L. S. B., 1971: New hominid skull from Bed I, Olduvai Gorge, Tanzania. *Nature* 232: 308–312.

LEAKEY R. E. F., 1971: Further evidence of Lower Pleistocene hominids from East Rudolf, North Kenya. *Nature* 231: 241–244.

LEAKEY R. E. F., WOOD B. A. 1973a: New evidence of the genus Homo from East Rudolf, Kenya II. *Amer. J. of Phys. Anthrop.* 39: 355–368.

LEAKEY R. E. F., 1973b: Further evidence of Lower Pleistocene hominids from East Rudolf, North Kenya, 1972. *Nature* 242: 170–173.

LEAKEY R. E. F., 1974: Further evidence of Lower Pleistocene hominids from East Rudolf, North Kenya, 1973. *Nature* 248: 653–656.

LEAKEY R. E. F., 2003: Further evidence of Lower Pleistocene hominids from East Rudolf, North Kenya, 1971. *Nature* 237: 264–265.

MARTÍNEZ L.M., LÓPEZ-AMOR H., PÉREZ-PÉREZ A., 2001: Microestriación dentaria y alteraciones del esmalte dentario en homininos Plio-Pleistocénicos de Laetoli y Olduvai (Tanzania). *Revista Sociedad española de antropología biológica* 22: 61–72.

MARTÍNEZ L. M., PÉREZ-PÉREZ A., 2004: *Post-mortem* wear as indicator of taphonomic processes affecting enamel surfaces of hominin teeth from Laetoli and Olduvai (Tanzania): implications to dietary interpretations. *Anthropologie* XLII, 1 (in this issue).

MOORREES C. F. A., FANNING E. A., HUNT E. E. 1963: Age variation of formation stages for ten permanent teeth. *J. of Dental Research* 42: 1490–1502.

PÉREZ-PÉREZ A., LALUEZA C., TURBÓN D., 1994: Intraindividual and intragroup variability of buccal tooth striation pattern. . *Amer. J. of Phys. Anthrop.* 94: 175–187.

PÉREZ-PÉREZ A., BERMÚDEZ DE CASTRO J. M., ARSUAGA J. L., 1999: Non-occlusal dental microwear analysis of 300,000-year-old *Homo heidelbergensis* teeth from Sima de Los Huesos (Sierra de Atapuerca, Spain). *Amer. J. of Phys. Anthrop.* 108: 433–457.

TOBIAS P. V., 1991: *Olduvai Gorge 4*: *The Skulls, Endocasts and Teeth of Homo habilis.* Cambridge University Press. 921 pp.

TRINKAUS E., 1995: Neanderthal mortality patterns. *J. of Archaeological Science* 22: 121–142.

WEISS K. M., 1973: Demographic models for anthropology. *Memoirs of the Society for American Archaeology* 27, *American Antiquity* 38, 2, part 2.

WOLPOFF M. H., 1979: The Krapina dental remains. *Amer. J. of Phys. Anthrop.* 50: 67–114.

WOLPOFF M. H., 1999: *Paleoanthropology*. Second Edition. McGraw Hill (Boston). 878 pp.

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